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Mouthing off about fish capture: Jaw movement in pinnipeds reveals the real secrets of ingestion

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Abstract

Determination of when and where animals feed and how much they consume is fundamental to understand their ecology and role in ecosystems. However, the lack of reliable data on feeding habits of wild animals, and particularly in marine endotherms, attests to the difficulty in doing this. A promising recent development proposes using a Hall sensor-magnet system, the inter-mandibular angle sensor (IMASEN) attached to animals' jaws to elucidate feeding events. We conducted trials on captive pinnipeds by feeding IMASEN-equipped animals with prey to examine the utility of this system. Most feeding events were clearly distinguishable from other jaw movements; only small prey items might not be resolved adequately. Based on the results of this study we examined feeding events from free-ranging pinnipeds fitted with IMASENs and dead-reckoners and present data on prey capture and ingestion in relation to the three-dimensional movement patterns of the seals.

Keywords: Feeding; Technology; Ecology; Harbour seals; Australian sea lions; Weddell seals

1. Introduction

Knowledge of when and where wild animals feed and how much they consume is fundamental to animal ecology (Elton, 1927; Lindeman, 1942; Krebs, 1978). Different methodologies have attempted to elucidate this in marine animals, including stomach temperature sensors (Wilson et al., 1992; Gales and Renouf, 1993; Gremillet and Pios, 1994; Wilson et al., 1995), oesophageal temperature sensors (Ancel et al., 1997), and jaw muscle sensors (Bornemann et al., 1992; Plötz et al., 2001). Temperature-based systems are limited to endotherms feeding on ectothermic prey, and all systems either lack fine resolution or are quite invasive. A recent development, however, the inter-mandibular angle sensor (IMASEN—Wilson et al., 2002), has been tested on a wide range of animals (Norgaard and Hilden, 2004; Ropert-Coudert et al., 2004) and promises to supercede most other systems (Wilson et al., 2002). It relies on a Hall sensor (Hall, 1879) attached to one mandible, which senses the

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magnetic field strength generated by a rare earth magnet attached to the other mandible with high resolution and at high frequency.

This paper assesses the utility of the IMASEN system for determination of feeding in pinnipeds. For this, captive animals equipped with the devices were fed prey of known mass and dimensions. The data obtained are contrasted to those obtained by free-living animals simultaneously fitted with dead-reckoners for describing the three-dimensional movements of the animals in the water column (Wilson and Wilson, 1988; Wilson et al., 2002). We outline the fortes and weakness in the system so that future users can benefit to the full from their subsequent deployment.

2. Materials and methods

2.1. Technology used

In this study, two different versions of the IMASEN (Driesen und Kern GmbH, Bad Bramstedt, Germany) were deployed. During the captive trials, a resin-embedded single channel logger with 8 MB flash RAM, 16 bit resolution with maximum dimensions of $73 \times 33 \times 19$ mm, and a weight of 35 g in air was used (Adelung et al., 2004). The Hall sensor ($6 \times 3 \times 2$ mm, KSY 10, Siemens GmbH, Germany) was also coated in resin and connected to the logger by a 4-strand cable and a plug.

In field-deployments, a slightly different version was used where the circuit board and battery were housed in a titanium cylinder (140×20 mm) with the cable exiting at one end via an O-ring seal. The cylinder was filled with silicon oil to negate problems with hydrostatic pressure on air spaces via a special, O-ring-sealed opening. The logger had a 16 MB flash memory, 16 bit resolution, and a weight in air of 86 g. The cable and sensor were identical to the one described above.

Both IMASEN units may be set to sample at frequencies of up to 30 Hz. The Hall sensor produces an output proportional to magnetic field strength intensity so that the proximity of a magnet can be well defined. In our application a slightly bent permanent rare earth magnet (Neodymium Iron Boron, $30 \times 25 \times 3$ mm, Vacuumschmelze GmbH and Co, Hanau, Germany) was placed under the seal's lower jaw, behind the mandibular symphysis while the Hall sensor was placed on top of the upper mandible, behind the nose so that, after suitable calibration, jaw angle could be determined to allow examination of feeding behaviour (see Liebsch, 2002; Wilson et al., 2002; Simeone and Wilson, 2003). The accuracy of the system depended critically on the placement of the magnet with respect to the sensor, but resolution of seal jaw angle to within 3 degrees would be typical.

The free-ranging seals also were equipped with a dead-reckoner (Driesen und Kern GmbH, Bad Bramstedt, Germany). This 12-channel logger recorded depth, swim speed, temperature (internal and external), light intensity (two different wavelengths), compass heading (three axes), body orientation (pitch and roll), and body position (Adelung et al., 2004). The logger had a 32 MB flash RAM, 16 bit resolution, and measured $90 \times 65 \times 28$ mm and had a weight of 140 g in air. The whole unit was potted in resin and could be programmed to record at frequencies of up to 6 Hz. Following the procedure described by Caruso (2000), animal heading was calculated based on the three-dimensional axes of the earths magnetic field resolved by the compass and corrected for body orientation of the animal recorded by the orientation sensors. Animal trajectory was then elucidated via vectors (Wilson et al., 2007), giving three-dimensional information about the animal's movements with positional information being calculated at intervals according to the logger sampling frequency. Potential errors in this methodology are discussed in Wilson et al. (2007).

2.2. Work on captive animals

Captive work was conducted at the Seal Centre, Friedrichskoog (Germany) and at Sea World Enterprises (Australia) during July 2003 and October 2001, respectively.

At the Seal Centre in Germany an adult lactating female harbour seal (*Phoca vitulina*), housed in a large pool (with ca. 280 m^3 of water) with underwater viewing, was trained through the process of positive reinforcement to be accustomed to the device-fitting process. For this it performed daily training and feeding sessions, during which it learnt to position itself next to a specific target (a ball on the end of a stick) at which point the technology could be attached. Attachment of the Hall sensor was complicated by seal anatomy: the head has loose jowls around the side of the mouth and the comprehensive covering of fur and generally loose skin meant that it proved difficult to select a site with minimal movement except for that involved in jaw opening. Finally, the sensor was placed on top of the nose, between nose and eyes, and the magnet under the lower jaw, behind the mandibular symphysis (Liebsch, 2002). The sites chosen were cleaned with acetone and dried off using a towel. The magnet, sensor and IMASEN (recording at 20 Hz) were glued to the fur using cyanoacrylate glue (Sekundenkleber, UHU GmbH, Germany) with the cable leading from the sensor on top of the nose between the eyes to the IMASEN, which was positioned on top of the animal's head.

A time check was made between the IMASEN and a digital video camera, which filmed the whole procedure by bringing a second magnet close to the attached Hall sensor five times in rapid succession. This signal was recorded by the IMASEN and the camera and allowed us to ensure synchronicity. The process was repeated at the end of the experiments. Then, to allow a calibration to be constructed between jaw-opening angle and Hall sensor output, the trainer slowly opened the seal's mouth and closed it again, while holding a measuring tape in front of the mouth while the process was filmed from the side.

Two separate feeding trials were conducted when herring (*Clupea harengus*) of differing sizes was fed to the seal. The size and mass of all fishes were noted before single items were thrown into the water to land about 1 m away from the camera in an under-water housing, positioned in the water about 5 m away. The seal was allowed to swim to the fish to catch it by which time it had generally sunk down directly in front of the camera, providing excellent side-on footage of the seal's prey handling. After ingestion, the seal turned around and returned straight to the trainer, awaiting the next round.

At the end of the trials, sensor and IMASEN were removed carefully by cutting them loose from the fur with a scalpel. The magnet came off after 2 days due to corrosion of the glue in salt water.

A comparable trial was conducted at Sea World Enterprises in Australia with a trained adult male Australian sea lion (*Neophoca cinerea*) in a circular pool of approximately 50 m diameter and 5.5 m depth (9580 m^3) feeding on different live prey items. The arrangement of sensor, magnet and logger on the sea lion was similar to that described for the harbour seal except that the sensor was attached farther down the nose, in the front third of the skull between nose and eyes. Only the angle calibration was conducted differently. Here, the sea lion held two sticks of different diameters ($\varnothing = 2.5$ and 6.0 cm) each for about 10 s in his mouth while the head was filmed from the side. The live fish, which were caught in the lagoon earlier and kept in a bucket of water, were measured (length and width) and their mass was determined before they were thrown into the pool one by one for the sea lion to catch. After each fish, the seal swam back to the side of the pool to the trainer, while the measurements of the next fish were taken. The fish species caught for this experiment were Tarwhine Bream (*Rhabdosargus sarba*), Butter Bream (*Parastomateus niger*) and Silver Whiting (*Sillago ciliate*). For positive reinforcement, the sea lion was fed with dead fish (mainly Yellowtail, Whiting, Herring, Mullet and Goatfish) or squid from time to time during the experiment.

The recorded logger-data from both harbour seal and sea lion were downloaded on a laptop computer. Subsequent inspection of the video footage allowed us to estimate the distances between the jaw articulation and the magnet and sensor (from the calibration procedure) so that we could calculate jaw-opening angle using standard trigonometry. These angles were then related to sensor output using curve-fits from Tablecurve 2D (v5.00, Systat Software Inc., USA) before the whole data set was transformed into jaw-opening angle (Liebsch, 2002). The video footage proved particularly valuable in identifying feeding events and relating certain patterns in the data to specific jaw movements. The calibrated data were analysed using MT–Beak (Jensen Software Systems, Laboe, Germany), which calculated maximum jaw-opening angle, duration and integral (under the angle–time curve) for every feeding event. These results were then compared with the measurements from the prey objects taken.

2.3. Work on free-ranging animals

During the Antarctic cruise ANTXXI/2 of the R.V. '*Polarstern*' 2003/2004, seven non-lactating female Weddell seals were equipped with IMASENs and dead-reckoners at the Drescher Inlet (72°52′S, 19°26′W) in the eastern Weddell Sea. At the time (early spring), the inlet was completely covered with sea ice, on which the seals lay close to cracks in the ice. The animals were immobilized for device attachment as described in Bornemann and Plötz (1993) and Bornemann et al. (1998). The Hall sensors and magnets were positioned exactly as described for harbour seals (see Section 2.2) while the IMASEN (set to record at either 6 or 10 Hz;

resulting in a maximum logging duration of 8.0 or 4.8 days, respectively) was placed on top of the animals' heads (Fig. 1), by gluing a base of mesh-net into the fur and attaching the loggers with hose-clamps. The dead-reckoners (set to record at 0.5 or 1 Hz; resulting in a maximum logging duration of 8.3 or 4.2 days, respectively) were attached to the backs of the animals behind their shoulders using cable ties to bind them to mesh nets glued to the fur. The glue used was fast-setting Araldite two-component epoxy (Ciba-Geigy Corporation, USA), whose curing time was accelerated during cold conditions by using a hair dryer powered by a small portable generator.

After the glue had set, the jaw-opening angle calibration was carried out, by taking pictures with a digital camera from the seal's head, side on, with it's mouth closed, 1/3rd open and 2/3rd open, while holding a measuring tape in front of the mouth. With these three positions, which were held for about at least 10 s so it produced a clear signal in the recorded data, the range of the most frequent jaw-opening angles was covered. Care was taken that all pictures were taken from the same angle and distance and that on each picture the sensor and magnet were clearly visible to facilitating subsequent analyses. The length and girth of the animal also were measured and the weight estimated before the antidote was applied and the recovery of the animal was supervised from a distance.

To retrieve the devices, the animals were immobilized again and the IMASEN and dead-reckoner taken off again by cutting the cable ties or loosening the hose clamps. As the sensor could not be removed, the cable was cut as close to the sensor as possible. Four seals were equipped more than once so in these cases only the sensor had to be glued on top of the previous one, while the bases could be used again to attach the IMASENs and dead-reckoners as described above. After the last deployment (a maximum of three deployments per animal) all loose parts of the bases were also removed, leaving only the epoxy in the fur, which would have been lost with the annual moult.

The recorded IMASEN data were processed in a manner similar to that described in the work on captive animals (Section 2.2). The dive data were analysed using MT-Dive (Jensen Software Systems, Laboe, Germany) and the swim routes calculated using MT-Route (Jensen Software Systems, Laboe, Germany). Based on the common time base used by both IMASENs and dead-reckoners, feeding events could be related to geographic positions, depth and movement patterns.

3. Results

3.1. Captive harbour seal feeding on dead prey

During the two trials, where a total of five feeding sessions were conducted, 61 dead Herring were fed to the seal. Their length ranged from 13 to 25 cm (mean: 20.7 cm; SD: 2.36) and their weight from 20 to 117 g (mean: 68.3 g; SD: 22.1; sum: 4.166 kg). Between 10 and 19 prey items (mean: 12.2) were given to the animal during each session, which

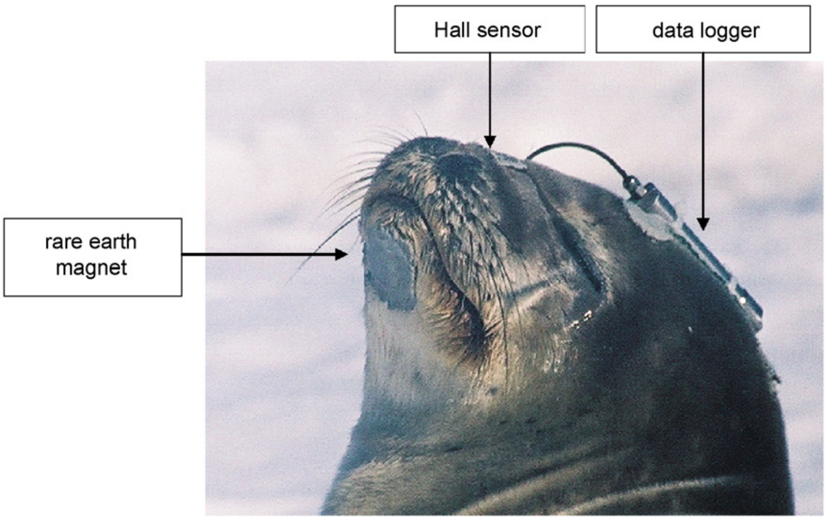

Fig. 1. Weddell seal (*Leptonychotes weddellii*) equipped with the IMASEN-system.

lasted between 8 and 15 min (mean: 11 min; sum: 55 min). All feeding events were clearly distinguishable in the recorded data (Fig. 2). Each prey handling event resulted in a specific pattern of jaw-opening angle over time (Fig. 3) consisting of two phases; a grab and handling phase followed by a swallowing phase. The first phase started with an initial, fast and extensive jaw-opening, producing the greatest angle for most of the feeding events, followed by a cascade of smaller, rapid peaks with decreasing maximum values and concomitant decreasing minimum angles in the troughs. The event ended after the jaw angle returned to the baseline representing a closed mouth. These signals related first to the initial snap of the seal to secure its prey before subsequent manipulation before the prey was swallowed head first. The swallowing phase consisted of a relatively slow jaw opening and closing,

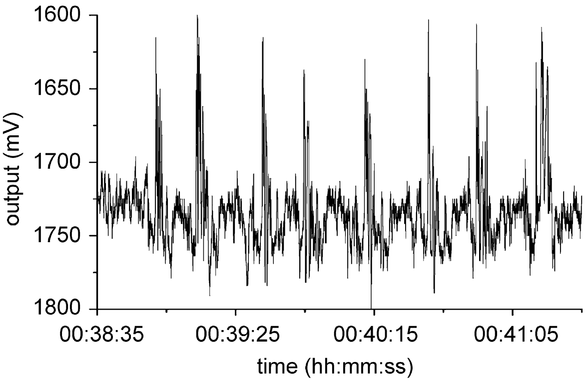

Fig. 2. Example of recorded magnetic field strength over time. Eight feeding events of a captive harbour seal feeding on dead herring are shown, where changes in jaw angle are represented by the variation in magnetic field strength.

producing a flat plateau in the jaw angle data whose maximum value was usually less than that recorded during the previous phases (Fig. 3).

The program MT-Beak calculated duration, maximum angle and integral (Fig. 4) of the jaw angle data over time for each feeding event, these being the main parameters defining feeding events (Wilson et al., 2002). The events lasted between 2.3 and 11.3 s (mean: 4.9 s; SD: 1.7). On average the maximum mouth opening angle was 26.7° (SD: 8.8) ranging from 10.8° to 45.8°. Values for the integral of the mouth opening angle curve over time ranged from 98.7° s to 1824.4° s, with a mean value of 534.0° s (SD: 356.7° s). Plots of all calculated parameters (duration, maximum angle and integral) against the measurements obtained from the prey items (weight and length) (Figs. 5 and 6) together with linear regressions (STATeasy 2000—J.L. Lozán, Germany) showed that the only significant relationship was that between fish length and integral (Table 1).

3.2. Captive Australian sea lion feeding on live prey

During the 25 min feeding trial, twelve live fish were given to the sea lion. After the first five fish caught, the animal ceased to be motivated to hunt the fish immediately and one fish managed to escape. This resulted in the seal spending considerably longer periods swimming after the prey before catching it. For those prey actually caught and ingested, the video clearly showed that, after getting a purchase on the food, the sea lion spent considerable time manoeuvring the fish into the right position before swallowing. Additionally, the

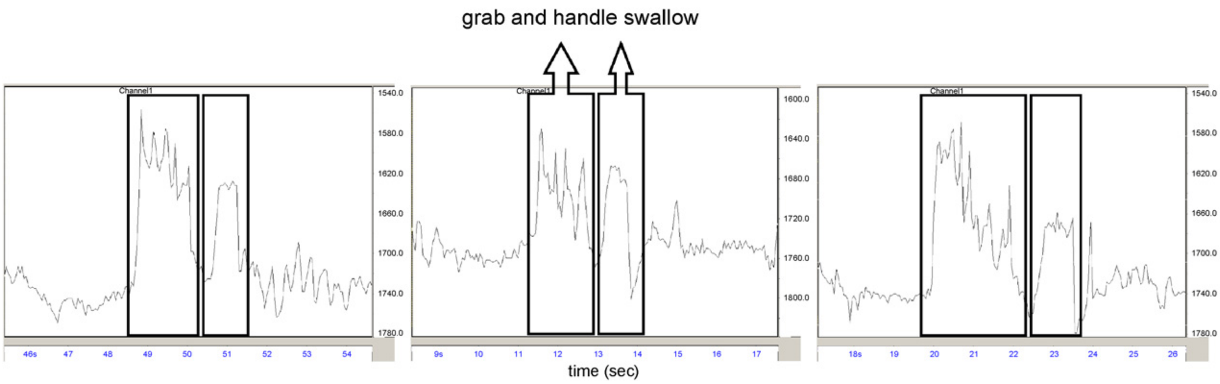

Fig. 3. Three examples of feeding events of a captive harbour seal feeding on dead herring, where the different phases of the events are marked in the logger-output data over time. The 'grab and handling' phase starts with an initial, fast and extensive jaw-opening followed by a cascade of smaller, rapid peaks with decreasing maximum values and concomitant decreasing minimum angles in the troughs. The 'swallowing' phase consisted of a relatively slow jaw-opening and closing, producing a flat plateau in the jaw angle data.

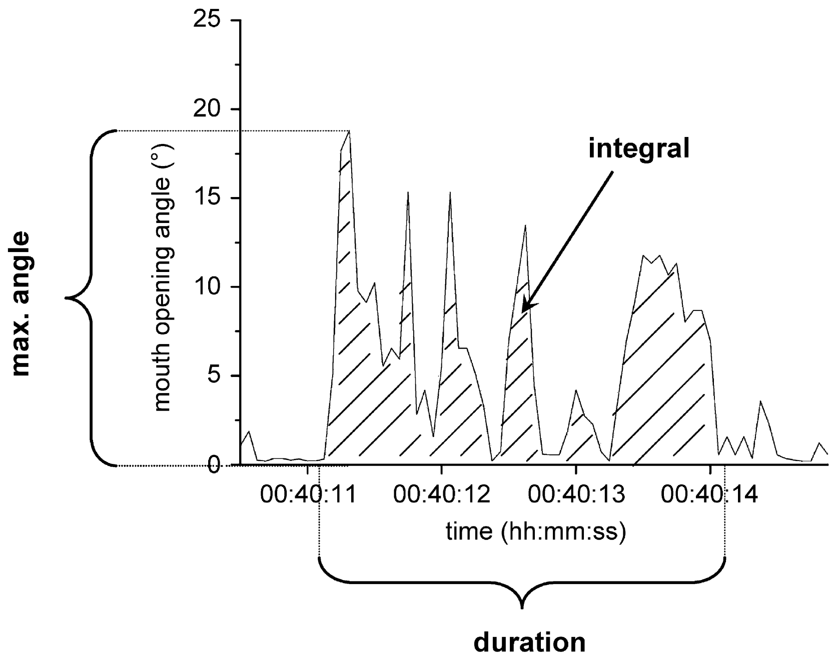

Fig. 4. Mouth opening angle curve over time of one feeding event of a captive harbour seal feeding on a dead herring. The parameters calculated by the analyses software, by which feeding events can be defined (duration, maximum opening angle and integral), are marked.

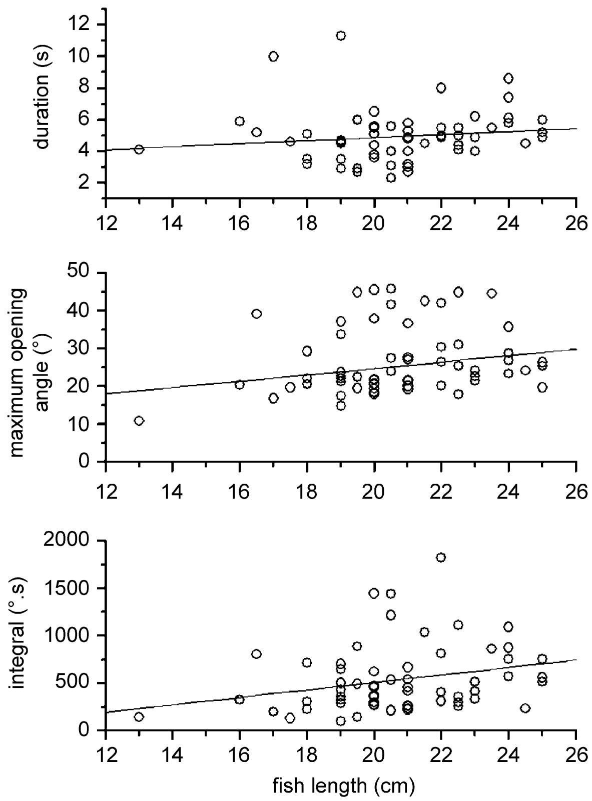

Fig. 5. Relationship between feeding event parameters (duration, maximum opening angle and integral) and fish length.

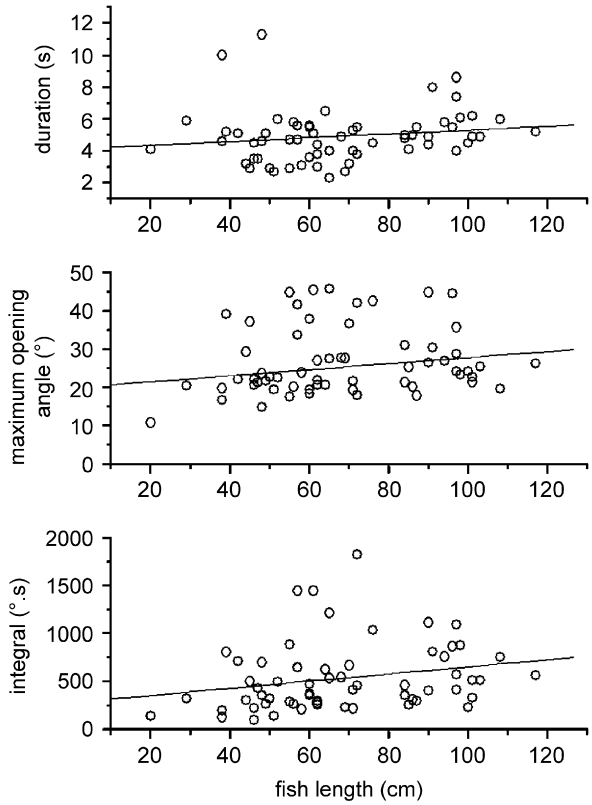

Fig. 6. Relationship between feeding event parameters (duration, maximum opening angle and integral) and fish mass.

Table 1
Linear regressions ($y = a + bx$) with statistic parameters obtained from STATeasy, for all calculated parameters (duration, maximum angle and integral) vs. the measurements obtained from the prey items (weight and length)

Parameters	a	b	F	r	Level of significance	P
Mass vs. duration	4.1154	0.0118	1.5162	0.1583	4.0036	>0.05
Mass vs. max. angle	19.9054	0.0791	2.2014	0.1881	4.0016	>0.05
Mass vs. integral	279.7892	3.7224	3.3708	0.2306	4.0016	>0.05
Length vs. duration	2.9601	0.0950	1.1248	0.1357	4.0016	>0.05
Length vs. max. angle	7.9370	0.8395	2.8682	0.2136	4.0016	>0.05
Length vs. integral	−280.3778	39.3643	4.3794	0.2608	4.0016	<0.05

Table 2
Prey and event parameters of the five analyzed feeding events from an Australian sea lion

Species	Silver whiting	Tarwhine Bream	Butter Bream	Tarwhine Bream	Tarwhine Bream
Weight (g)	67	167	88	123	158
Length (cm)	15	17	14	18	19
Width (cm)	5	7	9	7	8
Duration (s)	12.42	11.50	12.04	8.25	16.42
Max. angle (°)	40.9	39.2	43.8	39.9	35.1
Integral (°s)	5437	4358	4633	2945	5803

animal always returned to the surface whilst continuing to swim around, facing different directions, making it difficult to determine the exact time of prey ingestion. Only five feeding events, of the 12, could be used for analyses because the cable linking the sensor to the logger broke. For these, recorded ingestions lasted between 8.2 and 16.4 s, with a mean duration of 12.1 s (SD: 2.9). The average maximum opening angle was 39.8° (SD: 3.2°), ranging between 35.1° and 43.8°. The integral of the mouth opening angle curve over time, gave values ranging from 2945 to 5803° s, with a mean value of 4835.5° s (SD: 1111.3) (Table 2). A Tarwhine Bream, with the greatest length (19 cm), also took the longest to ingest (16.4 s) and had the greatest integral (5803° s) (Fig. 7A). The greatest opening angle of 43.8° was caused by a Butter Bream with the greatest width (9 cm) (Fig. 7B). Besides that there was no obvious correlation between any of the ingestion parameters recorded by the IMASEN (duration, maximum angle and integral) and the physical proportions of the fish (mass, length and width) (Table 2). During each feeding event most of the time was spent getting hold of the prey and handling it so as to get it into the right position to swallow (Fig. 7). Only the last set of peaks was presumed to be related to the actual swallowing of the caught fish (Fig. 7).

3.3. Free-ranging Weddell seals foraging

Altogether 13 deployments were conducted, during which two sets of devices got lost and in three cases either the IMASEN or the dead-reckoner malfunctioned due to battery failure or leakage in the battery housing. Nevertheless, a total of 20.47 days of simultaneous IMASEN and dead-reckoner data from six different animals was recorded. Data set duration ranged from 0.35 to 6.09 days (mean: 3.06 days; SD: 2.36; $n = 8$) depending on device functioning and time of recapture. Two data sets were excluded from further analyses because of their short duration (0.35 and 0.43 days) and because no feeding was observed. In the remaining six data sets, 508 feeding events were recorded. These events were mainly identified as a result of the patterns recorded from the captive harbour seal (see Section 2.2). However, the typical initial big, rapid peak in jaw angle, followed by a cascade of smaller ones until the mouth opening angle returned to values around zero were sometimes not as clear, probably due to the lower temporal resolution. Overall though, there was a strikingly similar apparent ‘grab and handling

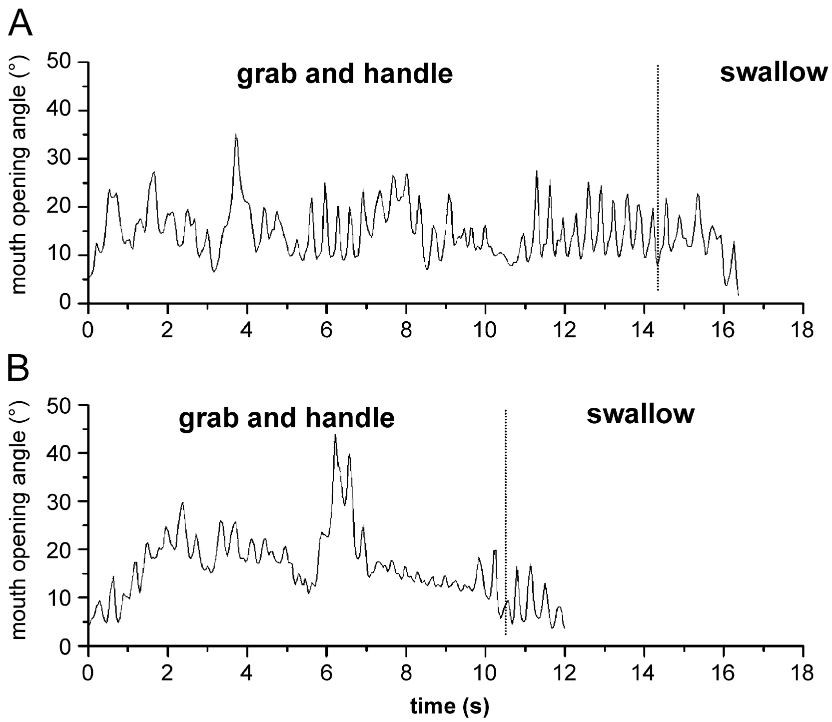

Fig. 7. Mouth-opening angle curve over time of an Australian sea lion feeding on: (A) Tarwhine Bream; and (B) Butter Bream. The different phases of ingestion ('grab and handle' and 'swallow') are marked as observed on the video footage.

phase' without the subsequent 'swallowing phase' as seen in the harbour seal (Fig. 8A and B). Jaw opening data had to be considered parallel with the dive data so as to be able to distinguish between putative feeding events (only occurring under water) (Fig. 8A and B) and other jaw activities such as ice reaming, vocalizing or yawning which occur above the water. It is notable, however, that these other activities produced patterns that were quite distinct from those that occurred underwater (Fig. 8C).

The variation in duration, maximum opening angle and integral was much greater than that encountered in the trials with the captive harbour seal. Events lasted between 0.6 and 30.7 s (mean: 2.8 s; SD: 3.1) and the maximum mouth opening angle ranged between 12.7° and 94.9° (mean: 37.9°; SD: 16.1) while values for the integral of the mouth opening angle curve over time ranged from 16.8° s to 7431.6° s, with a mean value of 431.5° s (SD: 639.4). An average of 2.8 feeding events were recorded per dive (SD: 3.1) with a range from 1 to 20. Most feeding events occurred between 60 and 140 m with a clear peak around 70 m (Fig. 9). The fewest number of events was recorded around 210 m and three small peaks seemed to occur around 250, 300 and 380 m, respectively. The feeding dives could be classified in most cases as either 'pelagic' (between 60 and 140 m) or more 'benthic' (below 300 m), with prey encounters mainly occurring during the bottom phase of these predominantly U-shaped dives. The majority of the feeding events showed a pattern consisting of only a few peaks (Fig. 8A) and occurred throughout the range of recorded water depth. A second pattern, which occurred 12 times of 508 supposed ingested prey items, was only observed during benthic diving, showed the same basic structure of a cascade of peaks but started with a greater amplitude and had much longer durations (Fig. 8B).

Small events in most cases followed impulses of increased swim speed and sometimes clear changes in tilt angle and heading (Fig. 10) whereas before large events hardly any indication of that kind was visible although they where systematically followed by a clear drop in velocity and considerable changes in tilt angle and heading (Fig. 11).

4. Discussion

4.1. Effects of the devices

Observations during the feeding trials and re-sightings of the equipped free-ranging animals

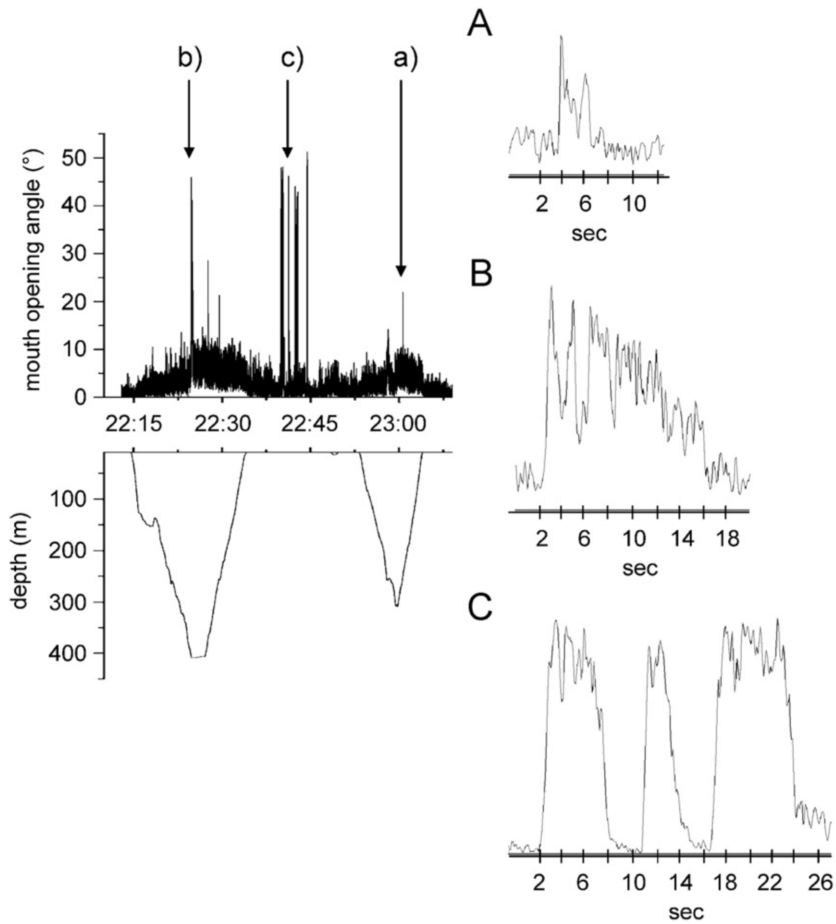

Fig. 8. Different patterns of mouth opening angle over time in relation to dive depth, representing different types of prey and other activities other than foraging: (A) Antarctic silverfish; (B) Antarctic cod; (C) ice-reaming.

during the deployment period, showed no obvious impact on their behaviour. In the captive animals this might be because they were trained, and accustomed, to carry all sorts of equipment. After the Weddell seals were equipped and the antidote had been applied, it took around 15 min until the first signs of activity were observed. Between 20 and 60 min after the immobilization, the first noticeable jaw movements appeared in the records of all but one animal. This period, lasting between 30 and 120 min, was characterized by series of peaks with varying amplitude and duration, representing unidentified jaw movements possibly due to the animal being temporally irritated by the devices although it might have been attributable to the anaesthesia. This behaviour was only observed at the beginning of a data set. One of the two seals equipped twice, displayed this behaviour each time, whereas the other did not show it during the second deployment. This may have been due to the animals adapting differently towards the impact of carrying devices or possibly to the anaesthesia. Overall, however, neither seemed to have a lasting influence on the animals nor hinder their performance.

4.2. *Utility of the IMASEN on pinnipeds*

Our trials using animals in captivity ended being rather less successful than we had anticipated. Three factors contributed to this.

Animals in captivity may not be motivated to feed in a manner similar to that found in the wild. A surplus of food coupled with a regular daily routine may lead animals to be rather disinterested in prey. This was particularly the case with the Australian sea lion. We assume that the extended mouthing and manipulating of food displayed by this animal is not typical of animals in the wild and this makes

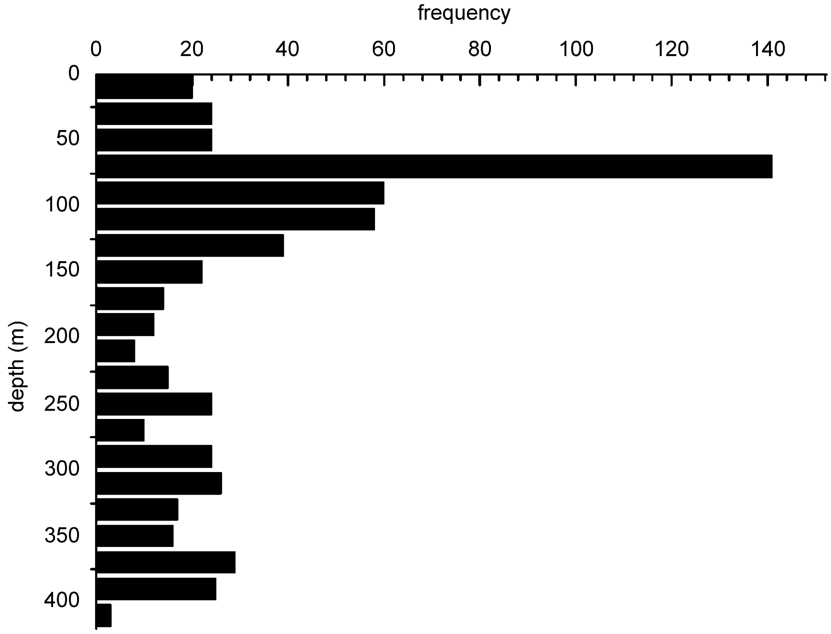

Fig. 9. Frequency distribution of feeding events over dive depth as recorded on free-ranging Weddell seals.

captivity/wild cross-border comparisons difficult. The harbour seal was clearly more motivated to feed, and did so rapidly and efficiently.

However, the conditions under which the harbour seal was fed mirrored those to which it was accustomed in captivity, namely those of being fed on a single prey species (herring) within a rather narrow size range. This leaves little room for prey-dependent variance in the jaw angle response over time, which may explain why attempted correlations were weak or non-existent. It should be noted that in the first presentation of this method on penguins, the size range of prey presented varied (in mass) by a factor of more than 250 (Wilson et al., 2002).

It is also difficult to ensure a large sample size in captive animals. The reluctance of many zoos to participate in this type of work coupled with uncooperative (and powerful) animals means that studies of this type on pinnipeds will almost always be carried out on just a few individuals.

Despite this, there are a number of levels indicative of prey ingestion, which we believe have been clarified by this study.

(i) Firstly, prey cannot be ingested without it being registered by the IMASEN. Thus, the most primitive condition is that the units will always signal that the jaw has opened, a necessary pre-requisite for feeding.
(ii) Secondly, jaw openings associated with ingestion are almost certain to be discernable from jaw openings where prey was not ingested. This is indicated by signatures in the jaw-opening angle over time indicative of an initial snap followed by manipulating and/or chewing before the prey was ingested. Only small prey items, which are ingested in one snap, might not be distinguishable from a failed attempt to catch prey. Additional information from other sensors, such as depth transducers may help in this matter.
(iii) A further stage involves determination of the mass of the prey ingested. This has proved equivocal in this study for reasons stated above. Indeed, the variance in the response shown by the harbour seal (Figs. 5 and 6) indicates that prey mass estimations may have considerable error. Nonetheless, there is little doubt that larger prey will generally result in a larger integral of jaw angle over time and more data are required on motivated animals fed on prey of a large size range to clarify the matter.
(iv) Finally, the work done in captivity has not helped elucidate whether different prey types may result in a different signature in jaw angle over time during handling and ingestion. This is a particularly exciting aspect of the work that also requires a good deal more work. There are,

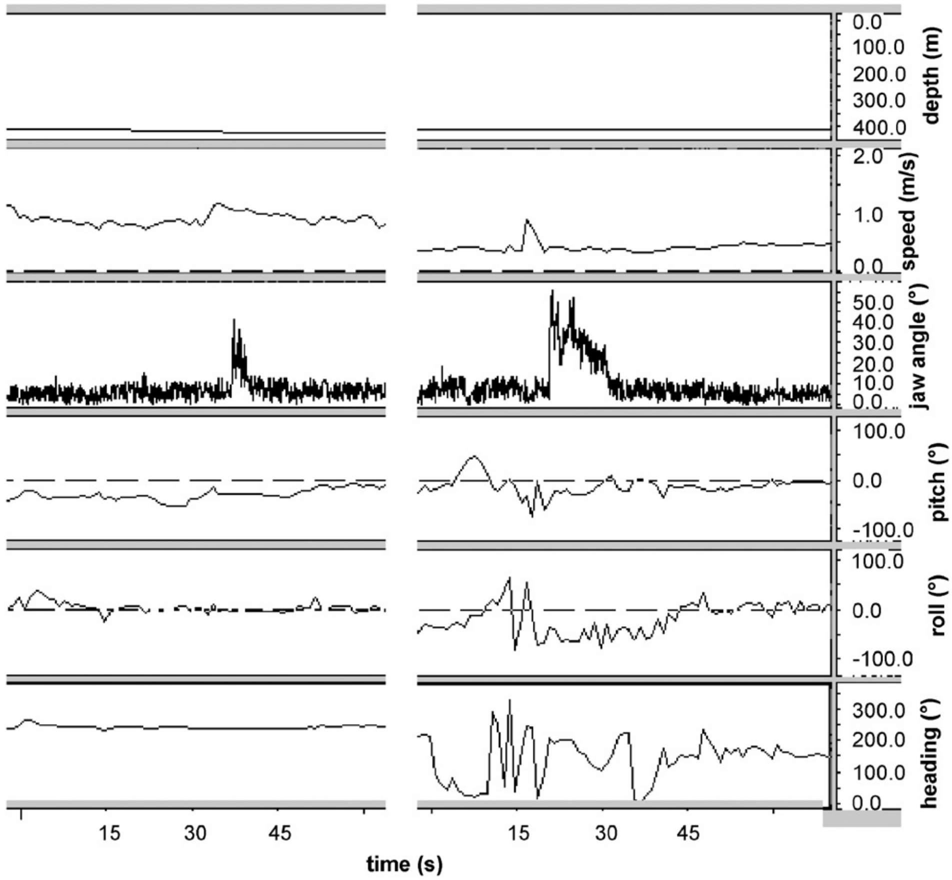

Fig. 10. Two examples for small feeding events (presumably Antarctic silverfish) together with dive depth, swim speed and three dimensional movement patterns.

however, indications from the studies done on the free-living Weddell seals that there are some cues that might be used to help differentiate prey types. If we assume that the identification of feeding events in Weddell seals can be based upon the patterns found in harbour seals (because both species are true seals with very similar anatomic features), the size range and morphology of herring fed to the captive animals corresponds closely with the predominant size of Antarctic silverfish (*Pleuragramma antarcticum*) (www.fishbase.org), a primary food source for Weddell seals in our study area (Plötz et al., 2001). Estimates of fish size (length) of the Weddell seals' prey, based on the calculated integral and the relation between integral and fish length acquired from the harbour seal, shows a clear peak in the frequency distribution between 10 and 15 cm (Fig. 12). Indeed, most estimated fish sizes were not bigger than 25 cm, which accords with the maximum size for Antarctic silverfish (www.fishbase.org) (cf. Fig. 8A). However, use of the same procedure and regression equation for some prey caught by the Weddell seals indicates a maximum fish length of 195 cm! Although this is obviously extremely unlikely it highlights a dichotomy in prey types (see Fig. 12), which apparently cannot be quantified by the same regressions. Indeed, the overall form of the jaw angle over time (Fig. 8), the location of prey capture in the water column and the different behaviour of animals feeding on such large prey (Fig. 11) augurs very strongly for a species other than *Pleuragramma*. The most likely candidate is Antarctic cod (*Dissostichus mawsoni*), which is a species also consumed by Weddell seals (Davis et al., 1999). Definitive proof is lacking and, given the problems of working in captivity, may be hard

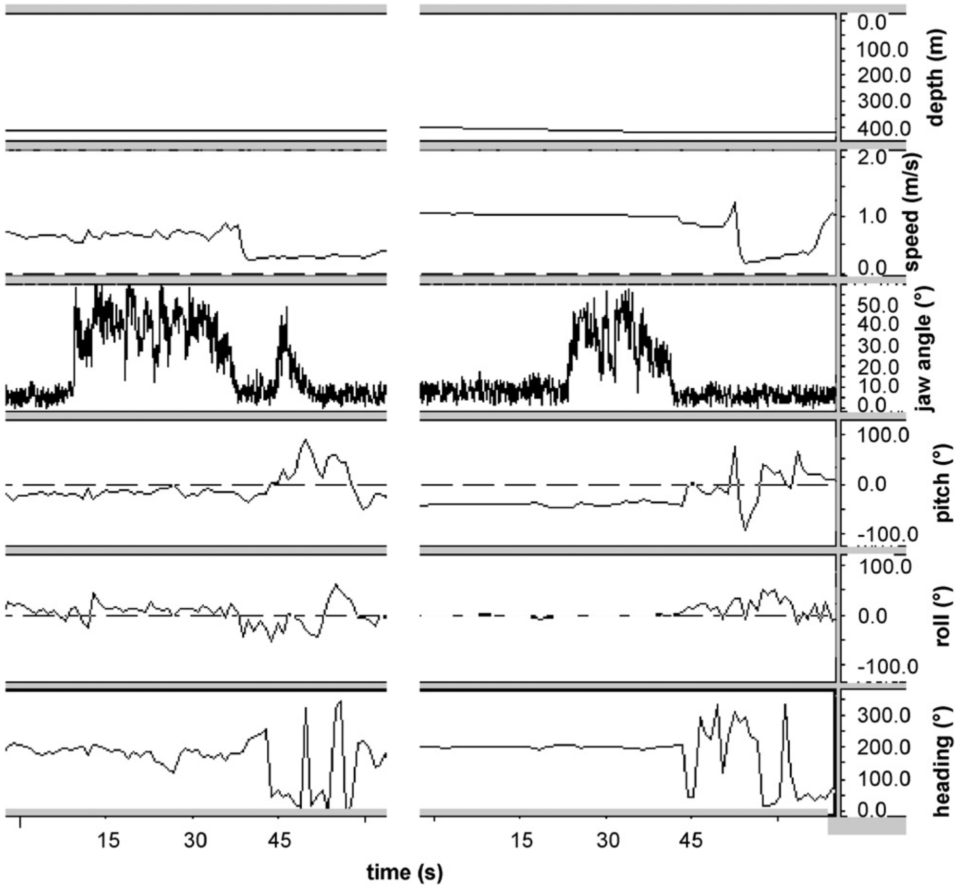

Fig. 11. Two examples for large feeding events (presumably Antarctic cod) together with dive depth, swim speed and three dimensional movement patterns.

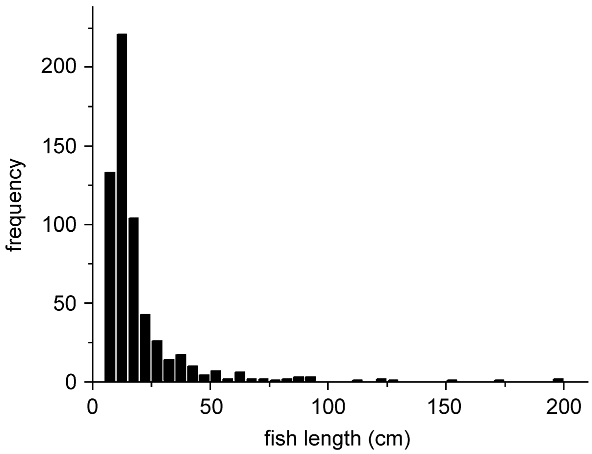

Fig. 12. Frequency distribution of estimated Weddell seal prey size, based on the calculated integral using the relationship between fish size and integral obtained from the trials on captive harbour seals (cf. Fig. 5).

to acquire. Perhaps short-term equipment of animals with video cameras (Davis et al., 2003) could be used to calibrate IMASEN signals with particular prey types in wild animals. Subsequently, the IMASENs could be used alone, presumably having much less impact on the animals (Walker and Boveng, 1995) and being able to be deployed for much longer periods.

Overall, therefore, the IMASEN system shows great promise for use on pinnipeds. It can identify prey ingestion events with reasonable certainty and larger prey items are likely to produce more dramatic jaw movements. We suggest that much more information on feeding could be obtained if the Hall sensor was also bound to a tri-axial accelerometer (cf. Wilson et al., 2007) so that head and jaw movements associated with prey capture could be used to build up a species-, or size- specific key. Although trials with animals in captivity are clearly useful, researchers need to be aware of their drawbacks. An alternative, albeit an onerous one, might be to equip free-living animals with IMASENs for foraging trips and undertake stomach sampling (Antonelis et al., 1987; Boness et al., 1994) immediately after they return to the colony. The most recently ingested prey will presumably be the least digested and it might be possible to work back through time in both prey swallowed and the IMASEN signals.

To our knowledge, the IMASEN system has been tried on 14 species of animal (Liebsch, 2002; Ropert-Coudert et al., 2002, 2004; Wilson et al., 2002; Takahashi et al., 2004; Wilson, unpublished) and it would probably be fair to say that the marine mammals are the most difficult to equip and interpret of the species thus far equipped. Part of this stems from the habitat in which they live which does not lend itself to easy study by man. However, the rewards for successful deployment are correspondingly greater and this should be reason enough for continued efforts to define and refine the IMASEN in this field.

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